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Article Addendum

A role for nautilus in studies of the evolution of brain and behavior

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Abbreviations: CS, conditioned stimulus; LTM, long-term memory; US, unconditioned stimulus; STM, short-term memory

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Nautilus is an ancient remnant of a largely extinct cephalopod lineage.[1] Its status within its clade is the subject of ongoing debate—its morphology, behavior and neuroanatomy may or may not be representative of an ancestral condition, and therefore its value as a model for ancestral cephalopods is uncertain. While the nautilus brain is simpler than that of more derived cephalopods[2] (coleoids), it is plausible that this is a secondary simplification related to ecology, and not a precursor to the vertebrate-like CNS of modern cephalopods. However, the absence of the vertical lobe complex, implicated in learning and memory in coleoids, makes studies of cognition in nautilus particularly interesting from a comparative perspective. Our research on the behavior and sensory biology of *Nautilus pompilius* gives the first indications of learning and memory in this ancient genus,[3] and suggests that even with a far simpler brain containing no clearly defined 'memory' center, nautilus performs simple cognitive tasks comparably to its more derived relatives.

The molluscan taxon Cephalopoda is a successful and diverse assemblage. Present since the Cambrian, cephalopods have undergone repeated radiations, extinctions and a relatively recent diversification into the several hundred soft-bodied species described today.[4] All modern cephalopods belong to one of two sub-classes, the ancient Nautiloidea or the more modern Coleoidea.[1] Coleoids have a large and centralized nervous system that supports a range of complex and plastic behaviors. Their brains contain two discrete lobes dedicated to learning and memory, the vertical and frontal lobe complexes, which display vertebrate-like properties[5-7] and are unique among invertebrates.

Nautilus brains are relatively simpler, containing fewer lobes and fewer neurons than coleoid brains.[2] The dedicated learning and memory centers present in the coleoid brain are absent in nautiloids, which may represent an ancestral condition. Alternatively it is plausible that the simple brain represents a secondary simplification relating to ecology. Either hypothesis suggests that studies of learning in nautiloid cephalopods may enlighten our understanding of general principles of the evolution of complex brains in response to selection on behavior.

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The Lure of the 'Living Fossils'

Nautilus is often listed among the ranks of the 'living fossils'—relict species that have persisted largely unchanged through millions of years of evolution, retaining not only ancestral morphologies, but perhaps also ancestral behaviors. Thus it is tempting to speculate that these species can offer a direct window into the evolutionary history of more derived relatives. While this is plausible, it is difficult, if not impossible, to discount alternative explanations for their 'primitive' appearance, such as secondary losses of complexity and convergence. Ancestral characters are not necessarily preserved as a set—while nautilus' chambered shell and lens-less eye are almost certainly pliesiomorphic, the status of its behavior and neuroanatomy are unclear.

Simple is not always ancestral, so what does this mean for comparative studies? While uncertainty regarding trait polarity in cephalopods complicates comparative studies, careful comparisons of behavior and neuroanatomy between the two subclasses can nonetheless be highly informative. We believe that nautilus can provide useful insights into the evolution of novel brain regions that support complex behaviors like learning and memory. The absence of a known analogue to the coleoid vertical lobe in nautilus provides a unique opportunity to examine the influence of close evolutionary history and divergent ecology on behavior.

Learning in Nautilus

Recent studies in our laboratory provide the first experimental evidence for learning in *Nautilus pompilius*.[3] Previously we characterized innate behavioral responses to olfactory[8-10]and vibratory stimuli,[11] but have focused recently on plastic behavior. The limited behavioral repertoire of nautilus makes developing procedures for conditioning difficult—measuring learning through a behavioral response requires a quantifiable and consistent behaviors, which are not overly abundant in nautilus. Initially we attempted aversive conditioning, pairing a simulated predator attack with a light-pulse, but this generated a 'freezing' response that resulted in cessation of measurable behaviors for long periods.[9] Instead we chose to focus on appetitive conditioning, utilizing nautilus' robust response to olfactory stimuli[10]—extension of the tentacles and increased ventilation rate. Cross-modal pairing of olfactory (US) and visual (CS) stimuli allowed us to use typical food oriented behavior as a measure of learning, while avoiding possible confounding effects of arousal in response to a CS of novel odor or tactile stimuli. Results indicated quite rapid learning (within ten training trials, spaced over 30 minutes), and expression of both short- and long-term memory. The temporal separation of the STM and LTM peaks was similar to responses to operant conditioning of predation in cuttlefish.[12-14] While a similar behavioral response in such a closely related animal seems unremarkable, it is surprising given that a different brain structure must be involved in memory in nautilus.

Pressures of Modern Life vs. Vestiges of the Past

Identifying values of plastic behavior for wild animals is difficult; the few studies of wild nautiluses suggest that unlike coleoids, they do not maintain a familiar shelter location or foraging area, and are scavengers rather than active hunters.[15,16] However, they lack active camouflage and an ink-sac, suggesting learned predator avoidance could be particularly valuable. Small-scale spatial memory may also be advantageous during foraging excursions into shallow water. While further laboratory studies provide a hypothetical framework for testing the adaptive value of learning in wild animals, field observations are needed for definitive answers.

Modern nautilids are predominately scavengers, yet it is likely that ancestral nautiloids occupied a range of ecological niches, occupying shallow- and deep-water habitats and hunting actively for live prey. Likewise the ammonoids, which are more closely related to coleoids than to nautilus, probably occupied predator niches.[17] Differences in behavior and ecology between nautilus and its ancestors suggest that extant nautiloids may in fact be dubious models for behavior of ancestors to either subclass.[18,19]

Conclusions and Future Directions

Coleoid cephalopods have yielded a wealth of information on convergent evolution of complex brains and behaviors. The vertical lobe complex of modern coleoids is most likely a recent development, concurrent with the changes in behavior and ecology that brought coleoids into competition with teleost predators in the Mesozoic.[20] Novel brain regions like the vertical lobe should arise only under sustained, directional selection on the behaviors they support, thus it is reasonable to hypothesize that behavioral plasticity was particularly advantageous for ancestors of extant coleoids. It is not clear whether the vertical lobe complex developed from an antecedent region that was also present in nautilus' ancestors, or whether nautiloids lacked the raw material from which the coleoid vertical lobe was derived. This is an intriguing question: There are considerable differences in morphology between the ancestors of each group that predate the appearance of coleoids, suggesting different niche occupancy and consequent optimization towards different behavioral phenotypes over a long period. By studying the neural bases of learning in nautilus, perhaps we can begin to understand the selective pressures that shaped neural substrates of learning in the two subclasses. We hope that the development of neurophysiological techniques suited to nautilus, coupled with ongoing, targeted behavioral assays, will provide new insights into the evolution of complex brains.

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